

Distributional Patterns of Juvenile *Mytilus edulis* and *Mytilus californianus*

BY

PETER S. PETRAITIS

Department of Biology, California State University, San Diego, California 92182

INTRODUCTION

Mytilus edulis Linnaeus, 1758 and *Mytilus californianus* Conrad, 1837 are two species of mussels which occur on the west coast of North America. *Mytilus edulis* is commonly found in bays and on semi-exposed coasts while *Mytilus californianus* is found only on exposed coasts (HARGER, 1967). Association of these species is assumed to be spurious since *M. edulis* and *M. californianus* are so similar. It has been suggested this coexistence is maintained by storms and selective predation which continually provide new surfaces for recolonization (HARGER & LANDENBERGER, 1971; HARGER, 1972).

In quiet bays, *Mytilus californianus*' exclusion has been attributed to physiological and competitive factors. The physiological inability of larval *M. californianus* to withstand salinity stress has been proposed as a possible determinant of exclusion (YOUNG, 1941). A very wide range of salinity tolerance has been shown for larval *M. edulis* (BAYNE, 1965).

HARGER (1968) suggests that exclusion of *Mytilus californianus* is caused by the upward crawling behavior of *M. edulis* which smothers the less mobile *M. californianus* under accumulating silt and pseudofeces. In bays with swift currents, less silt accumulates and *M. californianus* is found (HARGER, 1972).

However, there are several aspects of the distribution of *Mytilus californianus* which cannot be fully explained by either competitive or physiological factors. First, *M. californianus* is often not even found in bays of normal salinity (e.g. MACGINITIE, 1935). Second, Harger assumes *M. californianus* cannot compete after settling, yet shells of juvenile *M. californianus* are not found within mussel clumps from bays (PETRAITIS, 1974). Finally, settlement studies in bays never report juvenile *M. californianus* even on clean surfaces without *M. edulis* (e.g. GRAHAM & GAY, 1945; REISH, 1964).

If a population of a species is being held below the carrying capacity of the environment because of another species, there is a selective advantage to any gene which reduces or eliminates this sharing of resources (COLE, 1960). It would seem probable that the partition of the available space by *Mytilus edulis* and *M. californianus* can be explained by this hypothesis.

Both species are known to settle selectively. *Mytilus edulis* sets sequentially, first on filamentous algae and then into adult clumps (BAYNE, 1964). Without noting whether settlement is primary or secondary, small *M. edulis* have been found along the byssal threads of adults (SEED, 1969; DAYTON, 1971), on a variety of algae (COLEMAN, 1940; DEBLOK & GREELAN, 1958; SEED, 1969) and on newly exposed surfaces (MOORE, 1939). *M. californianus* have been reported to settle on barnacles (DAYTON, 1971), on old mussel shells (YOUNG, 1946) and on newly exposed surfaces (SHELFORD *et al.*, 1935).

Work was undertaken to clarify whether or not the species' differences in juvenile mussel distributions exist and if these differences could account for the known differences in adult distributions.

METHODS

All work was done at Crystal Pier in Pacific Beach and on a floating dock in Mission Bay unless otherwise stated. Both locations are in the San Diego, California area.

Distributional differences were examined by sampling twenty-six quadrats. Sampling was done by scraping off all mussels within a square which was approximately 56 square centimeters. Mussels were sorted by species and size. Since *Mytilus edulis* can grow to 7 mm in one month (COE, 1945) and *M. californianus* to 4 mm in one month (COE & FOX, 1942), mussels under 5 mm were designated as juveniles. Three of the samples were taken from the north jetty at the entrance of Mission Bay. Sampling dates, locations, and the number of adult and juvenile mussels per sample are given in Table 1.

Present address: Department of Ecology and Evolution, State University of New York, Stony Brook, N. Y. 11794

Juvenile differences in distribution were also examined by nearest neighbor methods. Pilings at Crystal Pier were chosen at random from those that could be reached at low tide. Sampling was done on July 2 and 3, August 16 and 27, September 15 and October 13, 1973. The September fifteenth data were taken at Scripps Institution of Oceanography Pier. A plumb line was placed on each piling. The species of all juvenile mussels that intersected the line and

the species of the next nearest mussel were recorded. Data collected after July 3, 1973 included the size of the nearest neighbor and the surface to which the juvenile mussel was attached.

In order to determine the relative abundance of substrate types, points along the plumb line were chosen at random. The surface type at each point and size of the nearest mussel were noted. These data were collected on February 8, 1974.

To test for the effects of adult mussels on settlement behavior, plastic ice cube trays with transplanted mussels were placed on the exposed coast and in the bay. The first experiment was conducted from July 6, 1973 to October 27, 1973. Five mussels of either species were placed in each cube. Four cubes were allocated for each of the three treatments: pure *Mytilus californianus*, pure *M. edulis*, and no mussels. Trays were covered with Varathane coated 0.63 cm ($\frac{1}{4}$ inch) mesh. Trays on the exposed coast were positioned at the mean tide level. Trays in the bay were suspended from a floating dock, 30 cm below the surface. At the end of the experiment, juveniles present were counted.

A second experiment was conducted from October 28, 1973 to March 6, 1974. In this experiment, seven mussels per cube and eight cubes per treatment were used.

RESULTS

Quadrat samples were analyzed by Spearman rank correlation. The number of juvenile *Mytilus edulis* per quadrat is correlated with the number of adult *M. edulis* per quadrat. Number of juvenile and adult *M. californianus* are also correlated. All other comparisons show no significant correlations (see Table 1).

Nearest neighbor data were tested by two way G test of independence (SOKAL & ROHLF, 1969). Analysis shows occurrence of juveniles depends on the presence of the same species (Table 2). For 129 of the 153 observations in Table 2, the juvenile is touching its nearest neighbor. The choice of substrate also depends on the species of the juvenile. Juvenile *Mytilus californianus* are found almost exclusively on *M. californianus*, while juvenile *M. edulis* are found on all types of surfaces.

Goodness of fit tests of the juveniles' utilization of substrate against the frequency of available substrate show a poor fit for both species (see Table 3, random point comparisons). Neither species settles randomly.

From the random point data, the mean length of the *Mytilus edulis* population (2.3 ± 0.30 cm) and of the *M. californianus* population (3.1 ± 0.77 cm) were estimated.

Table 1

Date, location and number of mussels per quadrat. Spearman rank correlations between abundances are given. Letters J denote juveniles; A, adults; M.e., *Mytilus edulis*; and M.c., *Mytilus californianus*. *P < 0.01.

Location and Date	Number of			
	AM.e.	JM.e.	AM.c.	JM.c.
Mission Bay Jetty	11	4	24	8
June 18, 1973	64	31	59	19
	40	2	37	3
Crystal Pier	51	37	20	14
June 18, 1973	73	21	10	5
Crystal Pier	0	0	53	27
July 2, 1973	64	12	35	10
	58	9	23	7
Crystal Pier	36	14	11	1
July 4, 1973	43	19	10	12
Crystal Pier	0	0	23	0
December 9, 1973	1	0	37	25
	1	0	12	6
	52	2	29	6
	44	7	35	10
	0	0	82	28
	1	0	21	4
	44	3	11	0
	45	2	18	4
	38	1	2	0
	0	0	31	0
	2	0	42	15
	0	0	11	0
	15	1	6	0
	0	0	0	0
	0	0	0	0
Correlation coefficients				
	AM.e.	JM.e.	AM.c.	JM.c.
AM.e.		0.880*	0.045	0.259
JM.e.			-0.009	0.272
AM.c.				0.706*

Table 2

Nearest neighbors of juvenile mussels on the exposed coast. Words in parentheses indicate relative levels of mortality observed by HARGER (1967). * $P < 0.01$. G denotes the G statistic (SOKAL AND ROHLF, 1969).

Base point	Nearest neighbor		G
	M.e.	M.c.	
Juvenile <i>Mytilus edulis</i>	56 (Low)	6 (High)	
Juvenile <i>Mytilus californianus</i>	9 (Low)	82 (High)	106.1*

Table 3

Comparison of substrate preferences of juvenile mussels on the exposed coast. Organisms in the 'other' column are predominantly barnacles. * $P < 0.01$. Degrees of freedom are denoted by df.

Base point	Substrate utilized			
	M.e.	M.c.	Other Living Organisms	Clear Surface
Juvenile <i>Mytilus edulis</i>	11	5	20	13
Juvenile <i>Mytilus californianus</i>	1	40	5	23
Random point	8	30	12	16
Comparison			df	G
<i>Mytilus edulis</i> versus <i>Mytilus californianus</i>			3	49.81*
<i>Mytilus edulis</i> versus random point			3	33.31*
<i>Mytilus californianus</i> versus random point			3	20.66*

A t-test of the mean length of the *M. edulis* population against the mean length of the *M. edulis* nearest to a juvenile *M. edulis* (0.8 ± 0.14 cm) shows significant differences ($P < 0.01$). Juvenile *M. edulis* are found among smaller *M. edulis* than are found on the average in the population. The same test comparing the mean length of the *M. californianus* population against the mean length of the *M. californianus* to a juvenile *M. californianus* (1.7 ± 0.71 cm) shows no significant differences. Juvenile *M. californianus* are found among *M. californianus* of similar length to those found in the population.

In the transplant studies (Table 4) the total number of mussels which settled in all cubes were counted. The data

were analyzed by a three way G test of independence (BISHOP *et al.*, 1975). Since some cubes were washed away, ten cubes were randomly chosen from each cell to equalize the cell size.

The choice of surface, the surface location and the species of the settler are not independent (Table 4, test 4). However, regardless of the surface, the species of the settler is independent of the surface location (Table 4, test 1). For both *Mytilus californianus* and *M. edulis* settlers, the choice of surfaces is also independent of surface location (Table 4, test 2). Finally, for a given area, either the bay or the exposed coast, the choice of surface depends on the species of the settler (Table 4, test 3).

Table 4

Occurrence of successfully settled juvenile mussels among artificial clumps of adults. Total number of juveniles, based on ten replicates, is given. In parentheses are the expected counts assuming species \times surface independence.

Location of Surface	Species of Settler	Surface		
		M.e.	M.c.	Open
Sea	<i>Mytilus edulis</i>	34 (22.7)	14 (28.0)	8 (5.3)
	<i>Mytilus californianus</i>	0 (11.3)	28 (14.0)	0 (2.7)
Bay	<i>Mytilus edulis</i>	7 (6.3)	8 (9.1)	4 (3.6)
	<i>Mytilus californianus</i>	0 (0.7)	2 (1.0)	0 (0.4)
Tests of Independence			df	G
Test 1. Location \times Species			3	7.38 n.s.
Test 2. Location \times Surface			4	3.31 n.s.
Test 3. Species \times Surface			4	56.68*
in the bay			1	3.21 n.s.
on the coast			1	53.47*
Test 4. Location \times Species \times Surface			7	167.16*

Note that a significant part of the deviations from species and surface independence is due to surfaces located on the coast. In bays, the choice of surface is independent of the species of the settler. On the coast, *Mytilus edulis* settles on *M. edulis* and open surfaces more often and on *M. californianus* less often than would be expected. *M. californianus* settles on *M. californianus* more often and on *M. edulis* and open surfaces less often than would be expected.

DISCUSSION

HARGER (1972) proposed that multiplicity of exposure, the periodicity and species dependent effect of storms, structural complexity of available surface and variation in predation allow for coexistence of *Mytilus edulis* and *M. californianus* on the exposed coast. While this may be the case in adult mussel populations, my observations suggest that very different substrates are acceptable for juveniles of these species.

On the coast, juvenile *Mytilus edulis* appear among *M. edulis* of a similar age or among other organisms such as barnacles. Juvenile *M. californianus* are found almost exclusively among older, more diverse (in length) clumps of *M. californianus*.

It is difficult to determine whether species differences in juvenile distribution are due to selective juvenile mortality, selective settlement, or both. Many claims of selective settlement have been based on inferences from the distribution of spat and the possibility of selective juvenile mortality has been ignored.

The only study comparing mortality of *Mytilus edulis* and *M. californianus* used large mussels (HARGER, 1967). Assuming for the moment that juvenile and adult mussel mortality are similar, the mortality differences described by Harger could not explain the distribution of juveniles observed in Table 2.

In exposed coastal areas, Harger found *Mytilus californianus* suffered higher mortality while *M. edulis* suffered lower mortality in mixed clumps than in pure clumps (HARGER, 1967, see Tables 94, 95 and 97). If mortality were the cause of differences in juvenile distribution, then the cell frequencies for juvenile *M. californianus* in Table 2 would be reversed. The distribution of juvenile mussels does not seem to be simply due to differences in mortality.

While differences in juvenile distributions may be maintained by selective settlement, the important question is whether or not these differences promote the association of *Mytilus edulis* and *M. californianus* on the coast. Lack of negative correlation between adults (Table 1) suggests adult mussels do not maintain small, pure clumps. It would seem that historical events randomize the mussel distribution and eliminate the juvenile differences. In spite of these events, differential juvenile settlement may allow each species a recruitment refuge, thus promoting co-existence by insuring recruitment.

In bays, juvenile *Mytilus californianus* are rarely found. HARGER (1968) proposes that the exclusion of *M. californianus* from bays is the result of competitive interactions with *M. edulis*. Yet the absence of juveniles even among the transplanted *M. californianus* suggests that exclusion is

not maintained by competition. The lack of juvenile *M. californianus* could be explained more simply in terms of low rates of successful recruitment into bays because of high larval mortality.

ACKNOWLEDGMENTS

I would like to thank Drs. Thomas A. Ebert, Richard K. Koehn and Douglas J. Futuyma for their comments on an early draft of the manuscript.

Literature Cited

- BAYNE, B. L.
1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journ. Animal Ecol.* 33: 513-523; 8 figs.
1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia* 2 (1): 1-47
- BISHOP, Y. M. M., S. E. FIENBERG & P. W. HOLLAND
1975. Discrete multivariate analysis. The M. I. T. Press, Cambridge, Mass.; 557 pp.
- COE, WESLEY ROSWELL
1945. Nutrition and growth of the California bay mussel (*Mytilus edulis diegensis*). *Journ. Exp. Zool.* 99 (1): 1-14; 2 text figs. (June 1945)
- COE, WESLEY ROSWELL & DENIS L. FOX
1942. Biology of the California sea mussel (*Mytilus californianus*). I. Influence of temperature, food supply, sex and age on the rate of growth. *Journ. Exp. Zool.* 90 (1): 1-30; 6 text figs. (5 June 1942)
- COLE, LAMONT C.
1960. Competitive exclusion. *Science* 132: (3423): 348-349
- COLEMAN, JOHN
1940. The faunas inhabiting intertidal seaweeds. *Journ. Mar. Biol. Assoc. U. K.* 24 (1): 129-183; 3 text figs. (25 January 1940)
- DAYTON, PAUL K.
1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389
- DEBLOK, J. W. & HANNIE F. M. GREELEN
1958. The substratum required for the settling of mussels (*Mytilus edulis* L.). *Arch. Neer. Zool. vol. jubil.*: 446-460
- GRAHAM, HERBERT WILLIAM & HELEN GAY
1945. Season of attachment and growth of sedentary marine organisms at Oakland, California. *Ecology* 26 (4): 375-386 (October 1945)
- HAROE, JOHN ROBIN E.
1967. Population studies on *Mytilus* communities. Ph. D. dissertation, Univ. Calif. Santa Barbara, 318pp.; Univ. Microfilms, No. 69-1719
1968. The role of behavioral traits in influencing the distribution of two species of sea mussel: *Mytilus edulis* and *Mytilus californianus*. *The Veliger* 11 (1): 45-49; 3 text figs. (1 July 1968)
1972. Competitive co-existence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. *The Veliger* 14 (4): 387-410; 8 text figs. (1 April 1972)
- HAROE, JOHN ROBIN & DONALD E. LANDENBERGER
1971. The effect of storms as a density dependent mortality factor on populations of sea mussels. *The Veliger* 14 (2): 195-201; 6 text figs. (1 October 1971)
- MACGINITTE, GEORGE EBER
1935. Ecological aspects of a California marine estuary. *Amer. Midl. Natur.* 16 (5): 629-765; 21 text figs. (September 1935)
- MOORE, H. G.
1939. The colonization of a new rocky shore at Plymouth. *Journ. Anim. Ecol.* 8: 29-38
- PETRAITIS, PETER S.
1974. Settlement patterns of *Mytilus edulis* and *Mytilus californianus* and their effects on the distribution of adult populations. M. A. thesis, Calif. State Univ. San Diego; 80 pp.

- REISH, DONALD J.
 1964. Studies on the *Mytilus edulis* community in Alamitos Bay, California: I. Development and destruction of the community. The Veliger 6 (3): 124 - 131; 4 text figs.; 1 map (1 January 1964)
- SEED, R.
 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. I. Breeding and settlement. Oecologia (Berlin) 3: 277 - 316
- SHELFORD, V. E., A. O. WESSE, L. A. RICE, D. I. RASMUSSEN & A. MACLEAN
 1935. Some marine biotic communities of the Pacific coast of North America, Part I. General survey of the communities. Ecol. Monographs 5 (3): 251 - 292 (July 1935)
- SOKAL, R. R. & F. J. ROHLF
 1969. Biometry. W. H. Freeman & Co., San Francisco, Calif. 776 pp.
- YOUNG, R. T.
 1941. The distribution of the mussel, *Mytilus californianus* in relation to the salinity of its environment. Ecology 22 (4): 379 - 386 (October 1941)
1946. Spawning and settling season of the mussel *Mytilus californianus*. Ecology 27 (4): 354 - 363 (October 1946)

